

**Phylogenetic and taxonomic considerations on the variability of cuticular surface micromorphology within one species, *Aphodius (Nialus) varians* Duftschmid (Insecta: Coleoptera: Scarabaeidae: Aphodiinae)**

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**Phylogenetic and taxonomic considerations on the variability of cuticular surface micromorphology within one species, *Aphodius (Nialus) varians* Duftschmid (Insecta: Coleoptera: Scarabaeidae: Aphodiinae) –** The polygonal microreticulation of the cuticular surface found in most Insecta and “Myriapoda”, in some Crustacea and even in the Loricifera is considered the basic cuticular surface pattern for all arthropodal, i.e. chitinous cuticulae for morphogenetic reasons. It is based on the economic close packing pattern of epidermal cells. The reticulation can be modified to an alveolate pattern by buckling the polygon surfaces possibly caused by the non-tensed epidermis during the deposition of the epicuticula. The elytra of different specimens of *Aphodius (Nialus) varians* Duftschmid (Insecta: Coleoptera: Scarabaeidae: Aphodiinae) show the reticulate pattern, the alveolate pattern and many transitional forms. Hence, the surface microsculpture is not constant within one species. Considering morphological and ecological results, the extreme alveolate form, *Aphodius (Nialus) venyigei* Endrődi, is downgraded to a morph of *A. varians*. Additionally, the first record of *Aphodius (Melinopterus) reyi* Reitter for Greece is given.

**Key-words:** Coleoptera - Scarabaeidae - *Aphodius* - Micromorphology - Taxonomy - Morphogenesis.

## INTRODUCTION

“Variation is not merely the spice of life,  
it is the very essence of living”.

(TURRILL 1952: 391)

In taxonomic literature, cuticular surface structures are often used as species specific characters in Coleoptera and other groups, but detailed descriptions or figures

of the cuticular micromorphology are usually lacking. Sometimes authors content themselves with attributes like "bright", "opaque" or "with/without microsculpture". Causal and functional aspects of surface patterns are generally neglected by taxonomists. As far as I know, in the pre-SEM time, only SCHULZE (1914, 1915; *Cicindela*, cf. also SCHULZE 1913), ZIMMERMANN (1917; Hydradephaga), NETOLITZKY (1935; general remarks), and BALFOUR-BROWNE (1940; Hydradephaga) carefully considered the microsculpture in Coleoptera from the taxonomist's point of view. Prior to these taxonomic studies NETOLITZKY (1911) had shown the usefulness of the cuticular microsculpture for pharmacognostic purposes, to identify the Spanish Fly. LINDROTH (1974; Carabidae), LARSON (1975; Dytiscidae), KHALAF (1980; various families), WOLFE & ZIMMERMAN (1984; Dytiscidae: Hydroporinae; perhaps following publications of WOLFE), and TAMURA & TAMURA (1986, 1987, 1988; Cerambycidae) carried out taxonomical studies on the cuticular microsculpture by SEM. Likewise MATTA & WOLFE (1981) showed some SEM photographs of the polygonal surface pattern in the species of *Hydroporus* (*Heterosternuta*) (Dytiscidae) but without giving detailed descriptions. In Thysanoptera, MOUND (1977) analysed the surface reticulation of many Glyptothripini. In the present paper, the variability of cuticular microsculpture within one species is shown. To determine the taxonomic and phylogenetic value of this character, the morphogenesis and the ecological-adaptive relations of the cuticular surface sculpture are reviewed.

## MATERIAL, METHODS, AND TERMINOLOGY

Specimens of *Aphodius* (*Nialus*) *varians* Duftschmid, *A. (N.) venyigei* Endrődi, and *A. (N.) rugosopunctatus* Petrovitz from different localities were studied. They are deposited in the following collections:

HFBC: Private collection of Dr. Hans Fery, Kornblumenring 107, D-12357 Berlin;

HNHM: Zoological Department, Hungarian Natural History Museum, Baross utca 13, H-1088 Budapest;

ISZP: Polish Academy of Sciences, Institute of Systematics and Evolution of Animals [the former Institute of Systematic and Experimental Zoology], ul. Sławkowska 17, PL-31-016 Kraków;

MNHG: Muséum d'Histoire naturelle, Route de Malagnou 1, CH-1211 Genève 6;

SMNS: Staatliches Museum für Naturkunde Stuttgart, Rosenstein 1, D-70191 Stuttgart.

Specimens were studied and photographed by means of the incident-light microscope Leitz Ortholux 3. Due to the necessity to study primary type-material, it was not possible to use an SEM to ensure comparability. The incident-light or metallurgic microscope is a workable alternative for the study of uncoated specimens. It is an old optical concept but is rarely used in the age of electron microscopy. Recently even a "rediscovery" of the metallurgic microscope for coleopterological purposes was published (SCHNEIDER 1990). The pros and cons of this method are discussed there. The extremely low depth of focus causes some difficulties to the interpretation

of three-dimensional structures. If convex or even tuberculous structures are photographed in oblique view, an irreal spatiality caused by the obliquity of the focus plane can result. The impression of the spaciality of surface structures can become very realistic by focussing during study.

The photographed individuals were collected and are deposited as follows:

- No. 1: ♂: Holotype of *A. venyigei* Endrődi. HUNGARIA, Berettyóújfalu, leg. L. Venyige 25.IV.1967; HNHM.
- No. 2: ♀: *A. varians* morph *venyigei*. GRAECIA, east of Igumenitsa, in sheep droppings, leg. H. Fery 13.IV.1984; HFBC.
- No. 3: ♂: Holotype of *A. rugosopunctatus* Petrovitz. ANATOLIA, Prov. Içel, Namrun, 1200 m, leg. C. Holzschuh 18.-22.V.1969; MHNG (coll. Petrovitz).
- No. 4: ♀: *A. varians* morph *rugosopunctatus*. POLONIA, Kraków, Sikornik, leg. Mazur 8.VI.1936, ISZP (coll. Mazur et Mazurowo).
- No. 5: ♀: *A. varians*. AUSTRIA, environs of Wien, leg. Baderle; SMNS (coll. Stegmann) [var. *fabricii* d'Orb.].
- No. 6: ♂: *A. varians*. AUSTRIA, Burgenland, Apetlon, leg. Ulbrich 17.V.1974; SMNS (coll. Ulbrich).
- No. 7: ♂: *A. varians*. AUSTRIA, Graz, leg. Mosbrugger, MHNG (coll. Petrovitz).

The terminology of the cuticular surface microsculpture was established in taxonomic descriptions. Typological taxonomists traditionally ignore morphogenetic or phylogenetic aspects of these patterns, their interrelations and transitions, and confine themselves to the classification of character states into separate, clearly discernable groups. HARRIS (1979) in his glossary of surface sculpturing works in the same tradition, but he tries to clarify and standardize the terminology, so his glossary is valuable. I adopt some of his terms, but the terms alone are not sufficient as they comprise no causal aspects. Instead, comparative descriptions of the patterns are necessary. HARRIS (l.c.) distinguished between micro- and macrosculpturing by the structures' visibility or invisibility at 100 x magnification. This may be practical but is not a biological criterion. A more heuristic criterion is used by BYERS & HINKS (1973). Those "having relatively large units, each being produced by an epidermal cell" are called "macro types", "those having smaller units, of which a number are produced by each cell" are called "micro types". However some sculpturings such as diffraction gratings can not be assigned clearly to one of these groups. But this does not affect us here. In the following I shall study only macro type sculpturings and the common scratched pattern, called aciculate by HARRIS (l.c.).

#### A CASE STUDY: *Aphodius (Nialus) varians* Duftschmid (INSECTA: COLEOPTERA: SCARABAEIDAE) AND ITS MORPHS

In the palearctic dung beetle species *Aphodius varians* we find morphs with different cuticular surface sculpture. The most extreme forms were described as distinct species (*rugosopunctatus*, *venyigei*). The elucidation of their ontologic and taxonomic status is the intention of the present investigation.

If we inspect the surface of the elytral intervals of these forms, we always find a reticulate pattern consisting of polygons. The polygons are sometimes convex and distinctly visible (alveolate pattern *sensu* HARRIS l.c.), sometimes flat and indistinct (reticulate pattern). Apart from these patterns, we find many small superficial scratches showing no preferential directions (aciculate pattern). On the pronotum, the reticular pattern is usually less distinct than in the elytra, but the scratches are very pronounced. In the following we shall study the different states of distinctness of these microsculptures in some individuals of *Aphodius varians* and some of its morphs (or related species ?). Although the taxonomic status of the taxa of the *A. varians*-group will be discussed later, we call them all morphs.

#### 1. DESCRIPTION OF THE CUTICULAR MICROSCULPTURE OF “*Aphodius venyigei* Endrődi” (figs 1-9)

In 1969, ENDRŐDI described *Aphodius venyigei* as a distinct species based on a single male specimen from Hungary. According to ENDRŐDI, it seems to be most closely related to *Aphodius varians*, but: “Die neue Art unterscheidet sich aber von dieser u.a. durch die Skulptur des Kopfes und der Flügeldecken und durch die Form des Kopulationsapparates auf den ersten Blick”. The aedoeagus (figs 30-31) which is in fact indistinguishable from that of *A. varians* will be treated below. The head of *A. venyigei* is very distinctly shagreened (“sehr deutlich chagriniert”; alveolate pattern), the elytra are shagreened, similar to the head, and totally flat (“ganz flach, ähnlich chagriniert wie der Kopf”). So, besides the flatness of the elytral intervals, the (micro)sculpture of the head and the elytra are the only two character states which distinguish it from *A. varians* (see below).

Indeed, in a series of *A. varians* s.l., *A. venyigei* is identifiable at first glance by its specific silky lustre, caused by the strong microsculpture of the flat elytral intervals (figs 1, 5). Could this peculiar microsculpture be a species-constitutive character state?

In fact, the polygons of the elytral intervals are most convex in *A. venyigei* (figs 2, 6, 9), and the intervals themselves are the flattest (figs 1, 2, 5), compared to all other morphs of *A. varians*. The scale-like shape of the polygons at the lateral parts of the photographs 1 and 5 is an optical artifact, but shows the three-dimensionality of the surface sculpturing. Around the interval punctures, the (mostly eight) polygons are arranged like the petals of a blossom (fig. 6). Scratches are very rare and short (figs 8, 9). The second interval of the holotype’s right elytron shows an irregularity, formed like an impression with radiating folds (fig. 1: IR).

The holotype’s (♂) pronotum is smooth with a reticulate sculpturing (fig. 3). Scratches are very rare. However, on the surface of the female’s pronotum the polygons are visible only on the margins of the points (fig. 7). The whole surface is covered with scratches. The sculpturing of the epicranium is slightly but distinctly alveolate (fig. 4).

A three-dimensional (alveolate) microsculpture also exists in the hollowed areas of the metasternum.

## 2. DESCRIPTION OF THE CUTICULAR MICROSCULPTURE OF “*Aphodius rugosopunctatus* Petrovitz” (figs 10-18)

In 1971 PETROVITZ described *Aphodius rugosopunctatus* as a distinct species based on one male specimen from Turkey. According to the original description this taxon differs from *A. varians* by the totally flat elytral intervals, the shagreened surface and a few other character states which are, however, highly variable in *A. varians* s.l. STEBNICKA (1982: 79) mentioned three additional specimens of this form from Poland and synonymized *A. rugosopunctatus* with *A. varians* without having explicitly considered the cuticular microsculpture.

The elytral intervals of the *A. rugosopunctatus* holotype are just as flat as in *A. venyigei* and the microsculpture is also very pronounced (fig. 16). However, their lustre is not silky but normally shiny (figs 10-11). The punctures are more impressed. Therefore the surface is slightly uneven (figs 10-12, 16). In the specimen from Poland, all the intervals except the sutural interval (SI) are strongly wrinkled and uneven (figs 17-18). The holotype shows more scratches in the intervals than *A. venyigei* (figs 15-16), but they are less distinct than in typical *A. varians* (compare figs 10-12 and 23+26).

The holotype's ( $\delta$ ) relatively smooth pronotum (not figured) shows an indistinctly reticulate pattern and some scratches.

## 3. DESCRIPTION OF THE CUTICULAR MICROSCULPTURE OF “TYPICAL” *Aphodius varians* Duftschmid (figs 19-29)

Generally the surface of *Aphodius varians* is very shiny. The polygons of the reticulation are clearly visible (figs 19-21), sometimes indistinct (fig. 26), sometimes hardly visible (figs 23-25). In summary, it can be said that there is a wide variability in the surface sculpturing. In specimen no. 5 the elytral surface seems to be very slightly alveolate (fig. 19). In specimen no. 7 the polygons are plane, their edges are sometimes carved like the scratches, especially their cranial and caudal edges (figs. 27-29). Specimen no. 6 shows a completely plane reticulation. The edges of the plane polygons are very fine (figs 24-25). The intervals of *A. varians* are more or less convex.

One pronotum ( $\delta$ ) is documented (fig. 22). The reticulation is not visible, but the scratches are frequent and extended.

## 4. COMPARATIVE SUMMARY

Summing up my observations, I postulate that the more convex the elytral intervals are the less visible is the reticulation, the more frequent and extended are the scratches, the more glossy is the cuticula seen with the naked eye. The extreme morphs, *A. venyigei* and the typical *A. varians*, show a clearly distinct appearance like many other closely related species in *Aphodius*, but there are transitional forms, too.

In the specimens investigated, I see no correlation between the surface pattern of the pronotum and the patterns of the other surface regions.

For the taxonomic interpretation of the present observations we have to explain the variability considering their morphogenetic causes and the possible consequences for the organism.

## THE CUTICULAR SURFACE MICROSCULPTURE: PHYSIOLOGICAL AND MORPHOGENETIC FUNDAMENTALS

### 1. THE RETICULATION

The polygonal, mostly hexagonal cuticular microsculpture, first recognized<sup>1</sup> by MEYER (1842), is the most common cuticular surface structure in the Insecta Ectotropha (= Ectognatha) (HINTON 1970, see also RICHARDS 1951: 267). KÖLLIKER (1858: 75) was the first to postulate that the contour of each polygon represents the contour of an underlying epidermis cell. Half a century later WARREN (1903) who studied the *Daphnia* integument (Cladocera) corroborated KÖLLIKER's statement. BLANEY & CHAPMAN (1969: 513) and HINTON (1970: 41) correlated the number of epidermal nuclei with the number of polygons in the same area of the insect integument. Their results supported KÖLLIKER's hypothesis for insects as well, which was confirmed by detailed histological (HEIMS 1956: 544) and morphogenetic studies (LOCKE 1967, LOCKE 1990). The cuticulin layer of the epicuticle (or the "outer epicuticle" sensu NEVILLE 1975, HEPBURN 1985) which forms the surface polygons alone (LOCKE 1967: 44)<sup>2</sup> is the first layer of a new cuticle to arise on the surface of the epidermal plasma membrane plaques. "The plaques are [...] determinants of cuticular surface patterns. The pattern over the epithelium comes from the surface presented by all plaques and depends upon the shape of each component cell." (LOCKE 1990: 197, cf. OKADA 1982: 99). The plaques' pattern depends on the pattern of the microvilli caused by the structure of the intracellular microfilamental apical web (see BEREITER-HAHN 1987: 23).

But why do the epidermal cells form a polygonal net? The hexagonal net is the most economic pattern for a close-packing of circles in a plane (for a detailed discussion of the geometrical fundamentals and additional references see MERETZ 1962, 1963). This close-packing pattern can be extrapolated to the dorsal surface of single-layered insect epidermis which could be considered in simplified terms to be a two-dimensional plane. If we understand the epidermal cells as pneus (sensu OTTO 1986: 74f) due to their hydrostatic pressure (BEREITER-HAHN 1986), their ideal close-packing results in six-sided prisms with hexagons at the interface, which is formed by

<sup>1</sup> in insects; to satisfy priority, it should be mentioned that in Crustacea, VALENTIN described and figured "sechseitige, dicht bei einander liegende Zellen" on the inner side of the outermost layer of the *Astacus* cuticle as early as 1836.

<sup>2</sup> However, HASS (1917) stated for *Gryllotalpa* (Caelifera): "Ist die Behaarung gering [...], so zeigt auch die Pigmentschicht [i.e. the layer beyond the outer epicuticle] eine bisweilen verzerrte, so doch deutlich erkennbare Felderung [i.e. polygons]".

the apical part of the epidermal cytoskeleton. The proximal plane shows different structures, e.g. dorsal feet, which do not matter here. HONDA (1983: 198) showed by photograph the result of vertical pressure of a plane single-layer of close-packed fat clay spheres: a regular hexagonal net on the upper and lower surfaces. Furthermore, a honeycomb pattern is formed when the boundary length of the cells is minimized by contraction of the microfilament bundles running along lateral boundaries of the epidermal cells (HONDA et al. 1986: 1; cf. DELHANTY & LOCKE 1990: 179).

If the epidermis does not form an ideal plane but a bulging shape, the ideal close packing net contains not only hexagons but also pentagons (see PYSHNOV 1980: 193; TARNAI 1984; OTTO 1986: 85) or other compensation figures as well. The densest spherical circle-packing is still a mathematical problem, known to mathematicians as the TAMMES problem (see e.g. TARNAI 1984 and CLARK & KEPERT 1986). As the insect integument contains very large bulges in relation to the small epidermal cells, i.e. a big radius of the sphere in relation to minute circles to be packed on the sphere, the ideal close packing pattern approximates a regular hexagon net where only a few compensating figures are necessary. During cell division, one hexagon turns into two pentagons at first. According to the model of PYSHNOV (l.c.: 190) "after any division two neighboring cells acquire one more side each, so pentagons become hexagons". Other models (ABBOTT & LINDENMAYER 1981) can explain the predominance of hexagons in many epidermal single-layers as well. As in every living system, however, the geometrical pattern of the arthropod epidermis during epicuticula secretion is not ideal. Mathematical models can only be approximations to explain our observations without the possibility for generalization or general predictability for other cases.

Summing up, the regular, polygonal net is the primary close packing pattern in the insect epidermis (constructional/morphogenetic constraint sensu REIF et al. 1985: 241). However, cytoskeletal and tension influences may modify this network into e.g. a scale like pattern, sometimes with a minute overlapping of the polygons; the polygons can be transversely elongate or form a zig-zag pattern (WOLFE & ZIMMERMAN 1984: 374-377) and so on.

Convexity or other three-dimensional surface sculptures of the polygons can be caused by simple buckling due to different rates of cuticulin secretion in different parts of the epidermal cell surface or by the surface shape of the epidermal cell during the cuticulin deposition (LOCKE 1967: 47), eventually modified by the smoothing and buckling actions of inter- and intracellular vacuoles (WIGGLESWORTH 1973; *Rhodnius*). In *Tenebrio molitor* the surface shape of the epidermal cells is of primary importance for building the cuticulin sculpture (DELACHAMBRE 1970: 393).

Hence, the cuticulin layer is a replica of the outer epidermal surface, showing the cell borders and the microvilli distribution (and their secretory activity!) at the epidermal apical plane. The folded surface of the elytral intervals of the *A. rugosopunctatus* from Poland (figs 17-18) was probably caused by the increased epidermal surface area in the intervals. The alveolate surface sculpture may be caused by the convex apical surface of the cells of the epidermis forming a non-tensed cell

sheet because of the increased surface area. This increase is either founded on mutation or on exogene physiological disturbance during metamorphosis.

To explain the correlations shown in the "Comparative summary" on page 269. I propose the following hypothesis. The epidermis of convex intervals forms a tensed cell sheet with plane apical cell surfaces. When the intervals are flat, their surface area is smaller. If their epidermal surface area is as large as in the case of convex intervals, the epidermis is no longer tensed. Hence, the apical cell surfaces are convex and their cuticular depositions form an alveolate pattern. The extreme case, an enlarged epidermal area in flat intervals is shown in the specimens of the morph *rugosopunctatus* from Poland. The intervals are folded and alveolate.

## 2. OBSCURING THE HEXAGONAL NET

The cuticulin layer is not the outermost cuticular layer in insects. After ecdysis the outermost layer is mostly the cement layer followed by the wax layer. The former is probably formed during or just after ecdysis, the latter just prior to ecdysis (NEVILLE 1975: 10f; HEPBURN 1985: 4f). The wax covers the cuticulin layer with its sculpture, "often obscuring microstructural detail" (HADLEY 1984), which was impressively demonstrated<sup>3</sup> in a black widow spider, *Latrodectus hesperus* Chamb. & Ivie (Araneae: Theridiidae), by HADLEY (1981) himself. The cement layer can obscure the surface pattern as well. As MALEK (1958: 266 and p. 20) points out the cement layer "fills in the depressions at the boundaries of the polygonal areas".

The wax layer is an important factor in controlling water movement through the cuticle and is protected against possible abrasive or impact damage by the cement layer. The thickness of both varies highly within arthropods, even in different parts of the same individual (HADLEY 1984, HEPBURN 1985). In the mature bloodsucking bug *Rhodnius prolixus* Stål (Heteroptera: Reduviidae), the wax layer is repaired after abrasion, the cement layer not (WIGGLESWORTH 1975). Consequently, lipid secretion forming the wax layer is feasible after ecdysis. Maybe it continues throughout the whole adult life, as supposed for *Schistocerca gregaria* (Forskål) (Caelifera: Acridoidea) by MALEK (1958: 567) and for *Periplaneta americana* (L.) (Blattaria: Blattellidae) by KRAMER & WIGGLESWORTH (1950, "presumably").

It is not known if in *Aphodius* the thickness of the wax layer and therefore the degree of obscuring reticulation is constant or changes during imaginal life. But the whole surface variability cannot be explained by simple variation of wax thickness because of the different degrees of convexity of the polygons.

In the studied specimens of the lamellicorn subfamilies Aphodiinae and Dynastinae, I frequently found many short and sharp cut-like fissures with upturned, ridge-like edges (figs 16, 24; fig. 78 in KRELL 1992: 346; aciculate pattern sensu HARRIS l.c.). It is not known how deep these fissures are. If they are only formed by the cement- and the wax-layer, they might be the results of contractions during the

<sup>3</sup> provided that the wax layers in spiders and insects are homologous.



solidification of the wax secretions. If they go deeper, then they could be the results of abrasions as shown by WIGGLESWORTH (1944). However, scratches caused by careless surface cleaning with a forceps (fig. 11) appear more like furrows than cuts. The first possibility is more likely because in a smooth reticulate pattern where the wax layer is distributed evenly over the whole surface, the scratches are more frequent than on the alveolate surface where the wax may be distributed mainly at the lower-lying borders of the polygons.

## PHYLOGENETIC AND TAXONOMIC VALUE OF THE CUTICULAR SURFACE PATTERN

### 1. HISTORICAL-PHYLOGENETIC ASPECTS

The polygonal macro-type sculpturing (sensu BYERS & HINKS 1973) is interpreted as plesiomorphic for insects by HINTON 1970 ("a fundamental or primitive pattern"). This is undoubtedly true because a polygonal surface pattern is also found in the Chilopoda and in the Progoneata, the presumable adelphotaxon of the Insecta (FUHRMANN 1922: 6-7<sup>4</sup>; EISENBEIS & WICHARD 1985: 128-155). Beyond that, equivalent structures are described in some Crustacea Decapoda, the "cuticular prisms" described e.g. by DENNEL (1947: 494-497), in the Ostracoda (OKADA 1981, 1982), furthermore in "nearly all terrestrial isopods"<sup>5</sup> (SCHMALFUSS 1978), in the Amphipoda Gammaridea (SAUDRAY 1972), and in the Cladocera (CLAUS 1876: 364, pl. 25; WARREN 1903; see also FREY 1987: pl. 5, fig. 64).

The polygonal surface pattern is the result of the cuticle deposition mechanism which works in the same way in all Arthropoda classes (GNATZY & ROMER 1984: 646; cf. OKADA 1982, LOCKE 1990) (and also in the Pentastomida (RILEY & BANAJA 1975)). Even in the Loricifera, whatever they are, the same surface pattern exists (KRISTENSEN 1983: 173f). "The honeycomb structure of the lorica, seen in both adults and larvae [...], is only a surface structure involving the outermost layer of the epicuticle [...]; the structure never involves deeper cuticular layers." (KRISTENSEN 1991a: 364). This could be an indication for the homology of the arthropod cuticle and the chitinous loriciferan cuticle (cf. KRISTENSEN 1991b: 244f). If it is only an analogy, it may be an indication for a constructional/morphogenetic constraint (sensu REIF et al. 1985: 241) of formation of a chitinous cuticle by an epidermal cell layer. The cuticle of Nematomorpha showing polygonal reticulation as well is a non-chitinous, completely different structure (BRESCIANI 1991).

<sup>4</sup> "Wie bei allen Chilopoden ist - im Gegensatz zu den Diplopoden - die kutikuläre Oberfläche der Antenne in unregelmäßige hexagonale Felder eingeteilt, deren jedes einer darunterliegenden Epidermiszelle entspricht, wie man besonders auf Tangentialschnitten feststellen kann." (p. 7). EISENBEIS & WICHARD (1984): 144-155) however, show the polygonal surface sculpture in Diplopoda as well. ATTEMS (1926: 49) denies (without giving reasons) any correlation between cell contours and polygons within the Diplopoda.

<sup>5</sup> if we are right in the interpretation that the "scales" are derivatives of the primary polygons or are induced by the constructional constraint of cuticular polygons, respectively.

The polygonal surface pattern as a plesiomorphic character state has no phylogenetical value to constitute monophyla within the Arthropoda. Maybe it can help to clarify the relationships of the Arthropoda.

The shaping, the modification, or the absence of a polygonal surface pattern is more interesting for taxonomic and phylogenetic analyses within lower categories. As shown above, however, the reticulate and the alveolate pattern are not distinct forms. They merge into one another.

## 2. ECOLOGICAL-ADAPTIVE ASPECTS

NETOLITZKY (1935) claimed that the microsculpture is a constant character of a taxon of the species-group: "Die Untersuchung dieser Mikroskulptur hat nun ergeben, daß sie für die einzelnen Arten und sogar für Rassen [sic!] konstant ist. Damit gewinnen wir ein neues und sehr wertvolles, wenn natürlich auch kein absolut zuverlässiges Merkmal (...)." Sometimes there is constant sexual dimorphism in the microsculpture, as in *Bembidion glaciale* (Carabidae): "die Weibchen besitzen sehr deutliche Netzmaschen auf den Flügeldecken, während die Männchen hier spiegelglatt sind." LARSON (1975: 264), however, noticed that in the water beetle genus *Hygrotus* (Dytiscidae) "females of certain species vary greatly in sculpture, punctuation and colour. Certain species include two forms of females, with some resembling the male in sculpture while others having the entire body covered with fine dense microsculpture." If the taxonomic interpretation of these females is correct, this is a case of dimorphism in the surface sculpturing. In *Hygrotus impresso-punctatus* (Schaller) transitional forms between the two morphs exist: "some females similar to males [without microsculpture on elytra], or with microsculpture restricted to apical one third of elytron; many females with dense microsculpture over entire disc of elytron" (LARSON l.c.: 276). MOUND (1977) stated an intraspecific phylogenetic oscillation of character states of the surface "reticulation" in leaf litter Thysanoptera. In the studied specimens of *Aphodius varians*, the cuticular microsculpture shows a wide non-clinal variability within one species. It is not always a constant species-specific character. Hence, its autecological significance may be very low.

Moreover it is not known if the thickness of the wax layer has any considerable effect on transpiration through the cuticle. "Attempts to correlate thickness of cuticular wax deposits and transpiration (...) have generally been unsuccessful (...)" (HADLEY 1977).

## THE TAXONOMICAL CONSEQUENCES: ON THE ONTOLOGY OF *Aphodius venyigei* Endrődi

### 1. CHOROLOGICAL AND ECOLOGICAL ASPECTS

Until now only two records of *Aphodius (Nialus) venyigei* Endrődi, 1969, have been published:

HUNGARIA, Berettyóújfalu [locus typicus] (47°14'N, 21°32'E; UTM ET43; under cattle pad, 1 ♂ leg. Venyige 25.IV.1967) (ENDRŐDI 1969).

HUNGARIA, Nógrádverőce [nowadays: Verőcsemaros], at the foot of the Börzsöni Mountains (UTM CT59), collector, number and sex of specimens not stated. From the same locality many records of *A. varians* are documented (ENDRŐDI 1979: 29).

ENDRŐDI (1979: 29) considered the species to be endemic in Hungary (“csak Magyarországon?”).

Dr. H. Fery, Berlin, discovered, syntopic with a great number<sup>6</sup> of “typical” *Aphodius varians*, two ♀♀ which show the characteristic silky lustre caused by flat intervals and alveolate microsculpture (see p. 268):

GRAECIA, east of Igumenitsa, in sheep droppings, 2 ♀♀ 13.IV.1984. (1 in HFBC; 1 in coll. Baraud, Toulouse, not seen).

Accompanying fauna: *Aphodius (Colobopterus) erraticus* (L.) [12 specimens], *A. (Acrossus) luridus* (F.) [12 spm.], *A. (Melinopterus) prodromus* (Brahm) [ca. 100 spm.], *A. (M.) reyi* Reitter [23 spm.]<sup>7</sup>, *A. (M.) stolzi* Reitter [14 spm.], *A. (M.) pubescens* Sturm [1 spm.], *A. (M.) consputus* Creutzer [2 spm.], *A. (Phalacrothous) paracoenosus* Balthasar & Hrubant [49 spm.], *A. (Ph.) quadrimaculatus* ab. *quadrisignatus* Brullé [17 spm.], *A. (Eudolus) quadriguttatus* (Herbst) [8 spm.]; *Caccobius schreberi* (L.) [4 spm.]; *Euonthophagus amyntas* f. *alces* (F.) [6 spm.]; *Onthophagus* (s.str.) *taurus* (Schreber) [1 spm.], *O. (Palaeonthophagus) lemur* (F.) [1 spm.], *O. (P.) fissicornis* (Steven) [19 spm.], *O. (P.) lucidus* (Sturm) [3 spm.], *O. (P.) sericatus* Reitter [50 spm.], *O. (P.) verticicornis* (Laicharting) [4 spm.], *O. (P.) ruficapillus* Brullé [19 spm.]; *Euoniticellus fulvus* (Goeze) [3 spm.]; *Copris hispanus* (L.) [2 spm.]; *Typhaeus lateridens* (Guérin) [1 spm.] (Fery det., teste Fery in litt. 10.IX.1990).

The syntopy with the “typical” *A. varians* indicates at least overlapping autecological requirements. However, syntopy allows no conclusions on the ontology of *A. venyigei*. It can indicate the existence of distinct morphs in one population or a character displacement of two sibling species in the same biotope.

Chorological and synecological data show no significant differences between *A. varians* and *A. venyigei*.

## 2. MORPHOLOGICAL ASPECTS

*Aphodius varians* is highly variable in colouration and surface microsculpture. As shown on pages 268-270 the degree of convexity of the elytral intervals is variable in *A. varians*, but on an average it is distinctly higher than in the two specimens of *A. venyigei*. The holotype of *A. rugosopunctatus* shows similar plane intervals.

ENDRŐDI's (1969) aedoeagus figure of *A. venyigei* seems to have been drawn from the dried object. In soaked condition (figs 30, 31), it shows no character which is outside the variability of the *A. varians*-aedoeagus. The epipharynx of *A. venyigei* lies in the range of variability of *A. varians* as well. It almost coincides with the figure in DELLACASA (1983: 293), but the epipharynx of the *A. venyigei* holotype shows seven short, thick bristles with cup-like base in the anterior region of the haptomerum (terminology after DELLACASA 1978). Three of them are mediadly displaced. Another

<sup>6</sup> 48 specimens preserved in HFBC.

<sup>7</sup> The distribution map of RESSL (1983: 107) shows no records between Turkey and Italy. I do not know any other records of this species from Greece, so *Aphodius reyi* Rtr. is new to Greece.

one of these bristles is situated among the finer bristles of the chaetopodium. The epipharynx of the *A. venyigei* ♀ bears only two thick bristles at the left margin of the anterior region of the haptomerum and a caudomedial row of three thick bristles among the fine ones of the chaetopodium. These patterns are within the variability of *A. varians*. The number of the thick bristles of haptomerum and median part of the chaetopodium is highly variable and generally shows no bilateral symmetry. The author is not able to verify DELLACASA's figure which shows no thick haptomerum bristles.

The lock and key hypothesis as mechanical isolation mechanism between species has been sufficiently refuted (cf. EBERHARD 1985). Moreover it is commonplace that the genitalia of different species need not be perceptibly different. So the aedoeagus gives us no indication for the ontology of *A. venyigei*. The other morphological differences are extreme states of a continuous variability. If the silky lustre of *A. venyigei* has any biological effects on this morph apart from being recognized by taxonomists cannot be settled at the moment. There are no reasons to diagnose *A. venyigei* as a biological species.

### 3. THE TAXONOMICAL STATUS OF *Aphodius (Nialus) venyigei* Endrődi, 1969

Except for the distinguishable appearance of the extreme varieties there is no reason to consider *A. venyigei* a distinct species. Therefore I downgrade *Aphodius venyigei* Endrődi, 1969, to the infrasubspecific status of a morph:

#### ***Aphodius (Nialus) varians* Duftschmid, 1805, morph *venyigei* Endrődi, 1969**

This is in fact a synonymization, but to obtain further information on *A. venyigei* in future, I sustain this name in the infrasubspecific category of a morph. Furthermore this name keeps species rank in the author's revision of Middle European Lamellicornia (KRELL & FREY 1992: 234) as most taxonomists do not take the infrasubspecific categories seriously.

For the same reason it may be opportune not to treat *Aphodius rugosopunctatus* Petrovitz as a simple junior synonym of *A. varians*, but to grant it infrasubspecific status of a morph instead. Before this (unprotected) nomenclatural-taxonomical act can be carried out, the types of the other morphs of this species (*punctatellus* Mulsant, 1842; *punctulatus* Mulsant & Rey, 1869) have to be studied if they still exist. DELLACASA (1988: 387) considered *A. rugosopunctatus* to be identical with the morph *punctulatus*, the latter having priority. In the present paper I am satisfied with the nomenclatural sloppiness to write about the "morph *rugosopunctatus*".

### OUTLOOK

By means of light microscope techniques, we cannot find significant diagnostic differences between *A. varians* and *A. venyigei*. However, these two forms are easily distinguishable with the naked eye because of the typical silky lustre of the latter. This silky lustre may indicate any micro-type surface sculpturing (sensu BYERS

& HINKS 1973). These structures are not visible by light microscopy but may have an eminent influence on the mode of light reflection. If more material of extreme forms of *A. varians*, especially of *A. venyigei* becomes available, SEM studies will be the only way to obtain further results. Another elucidating experiment would be the removal of the wax layer with solvents.

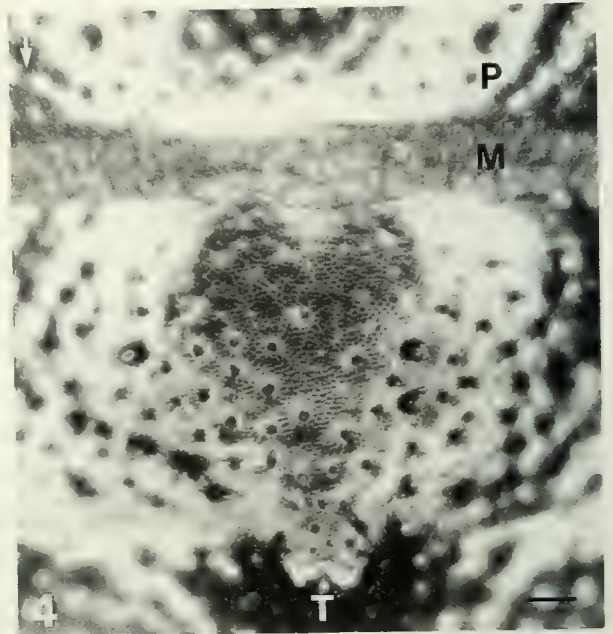
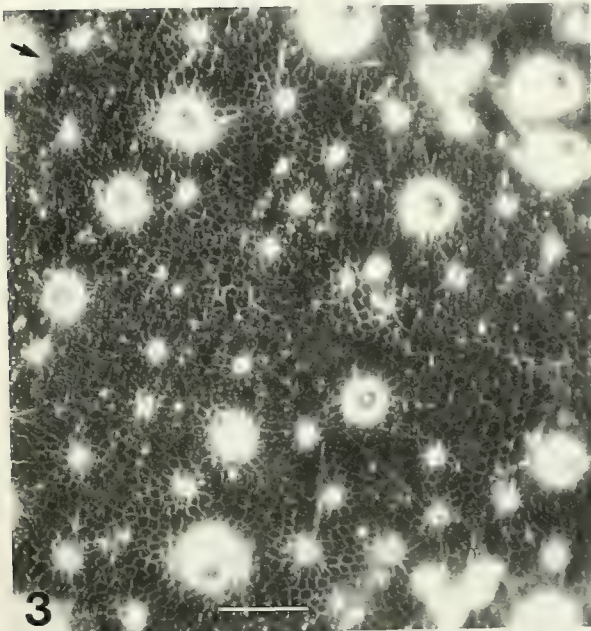
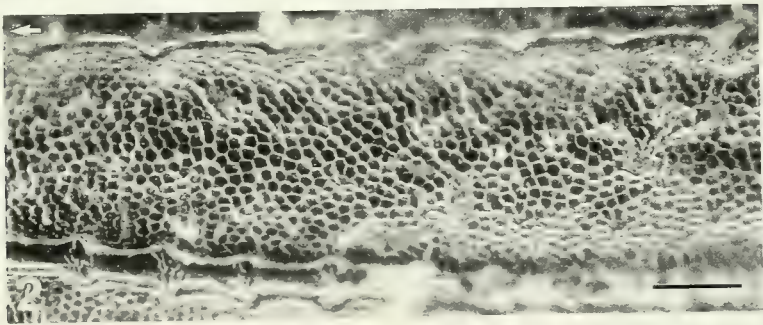
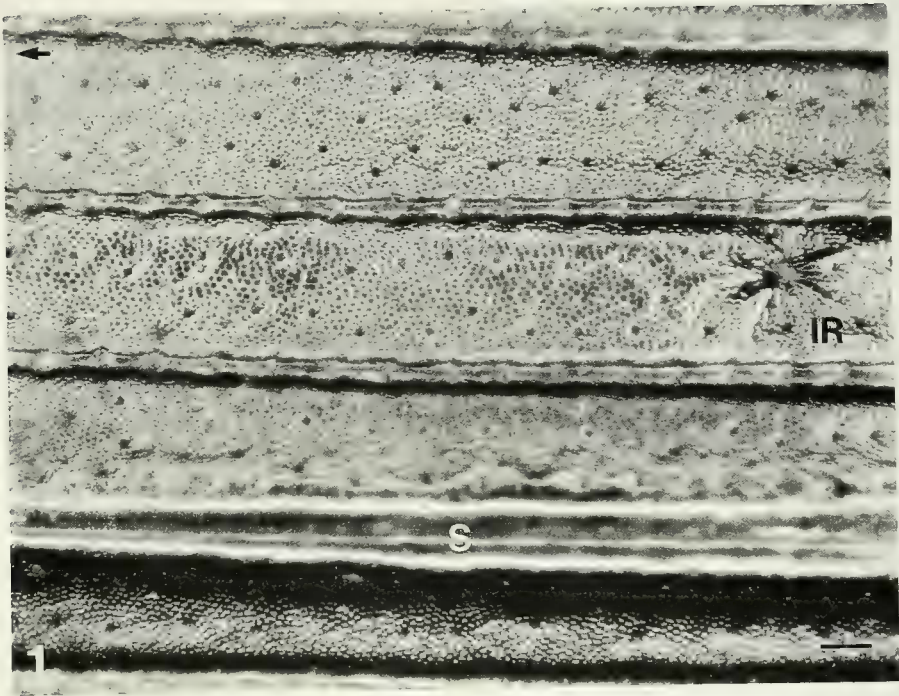
Taxonomists should investigate the intraspecific variability of surface microsculpture to evaluate the taxonomic weight of this frequently superficially used character within their groups. Bearing in mind that a polygonal surface pattern is basic, likely in most cases plesiomorphic, an analysis of this character might result in taxonomic reinterpretations.

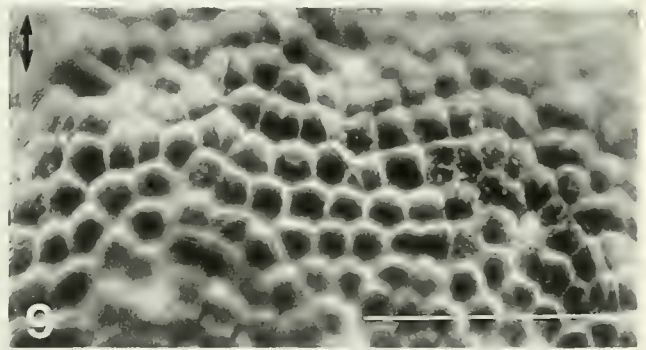
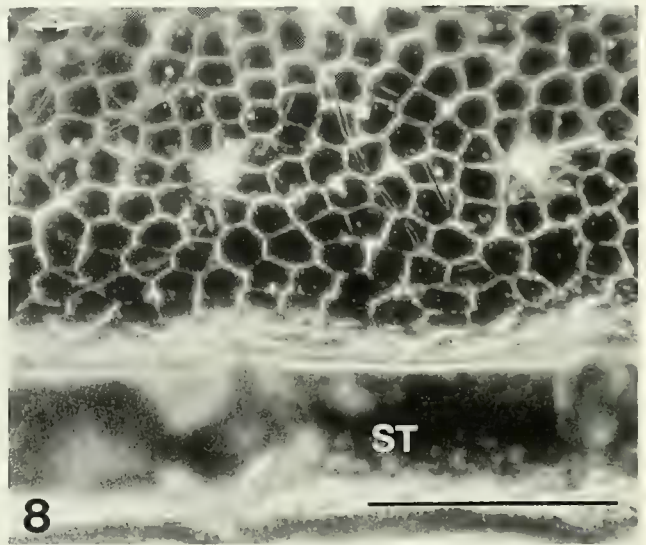
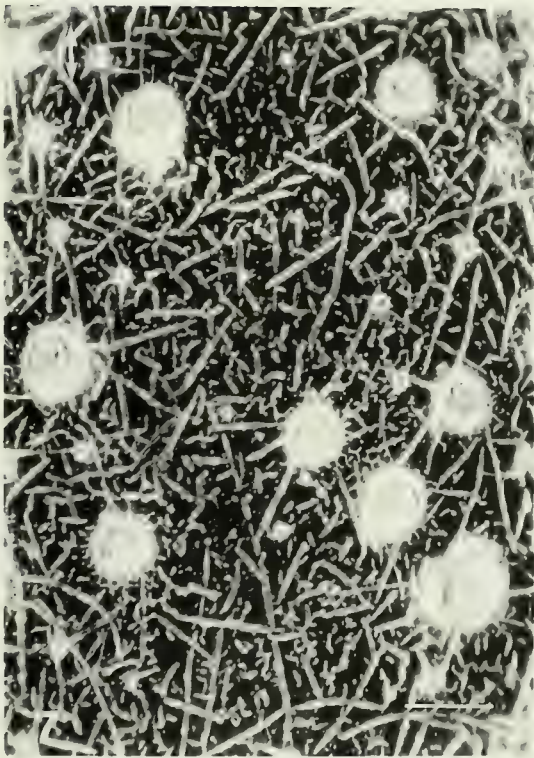
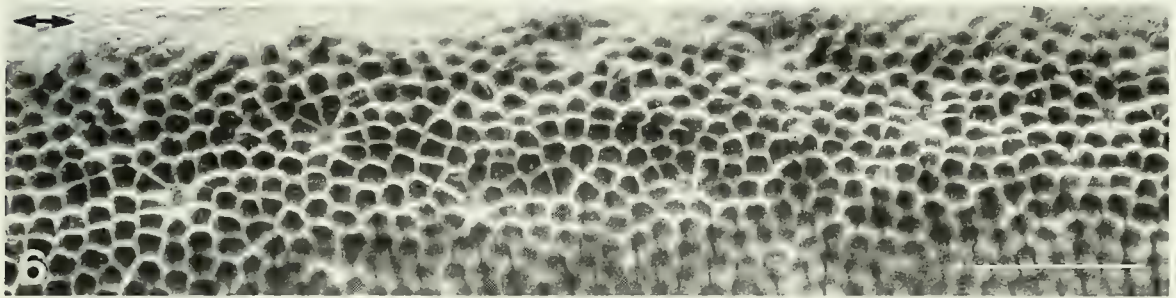
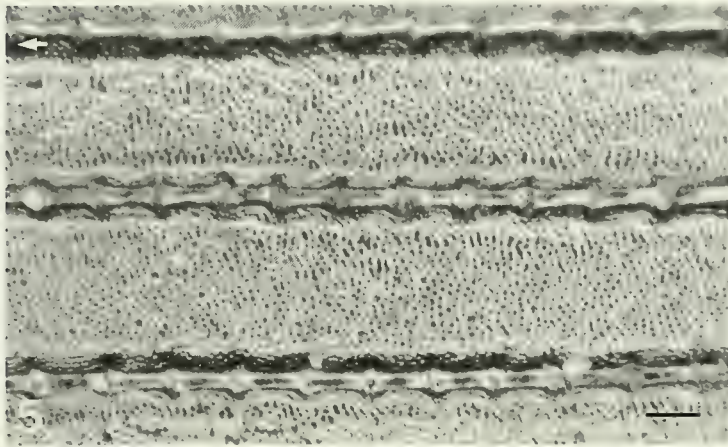
#### ACKNOWLEDGMENTS

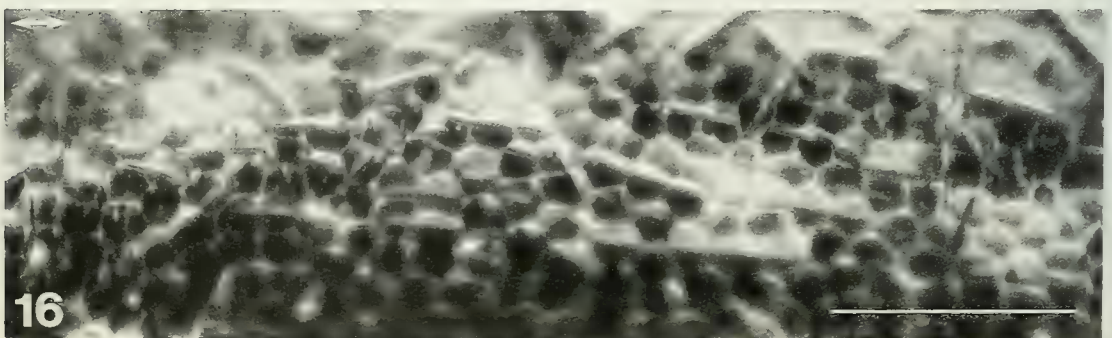
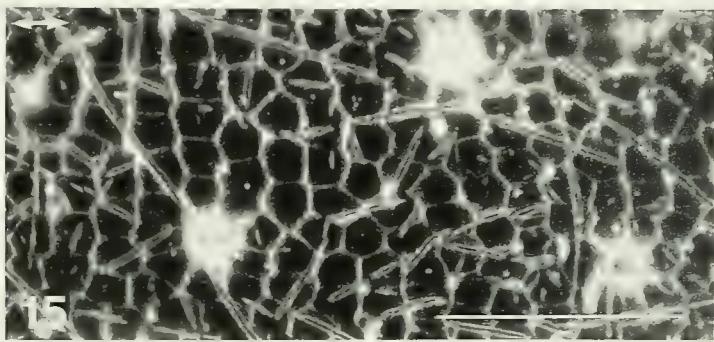
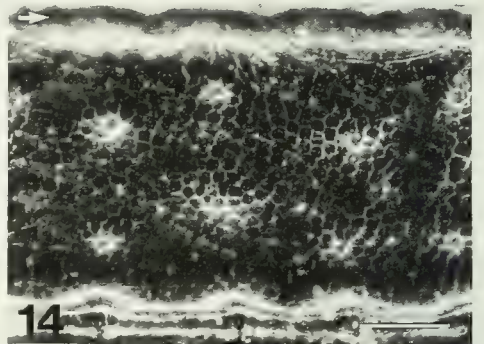
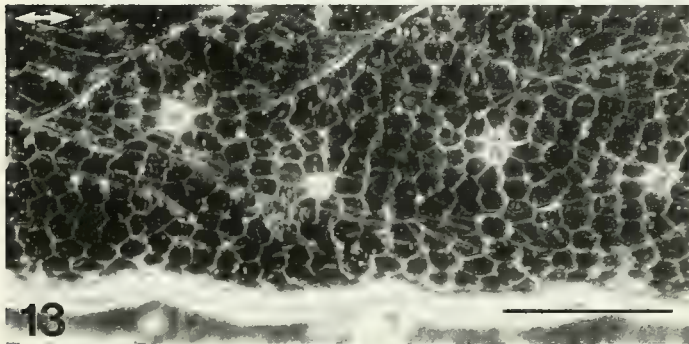
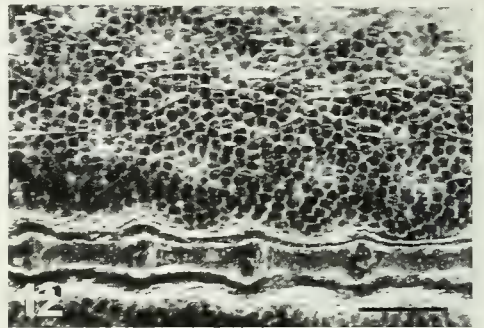
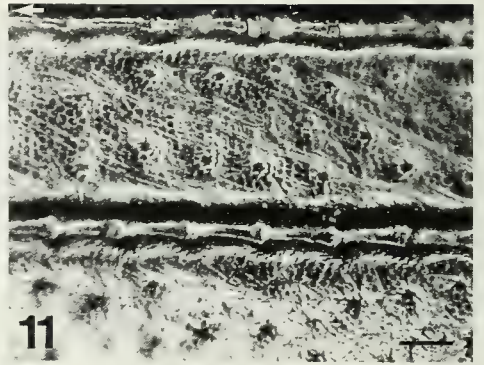
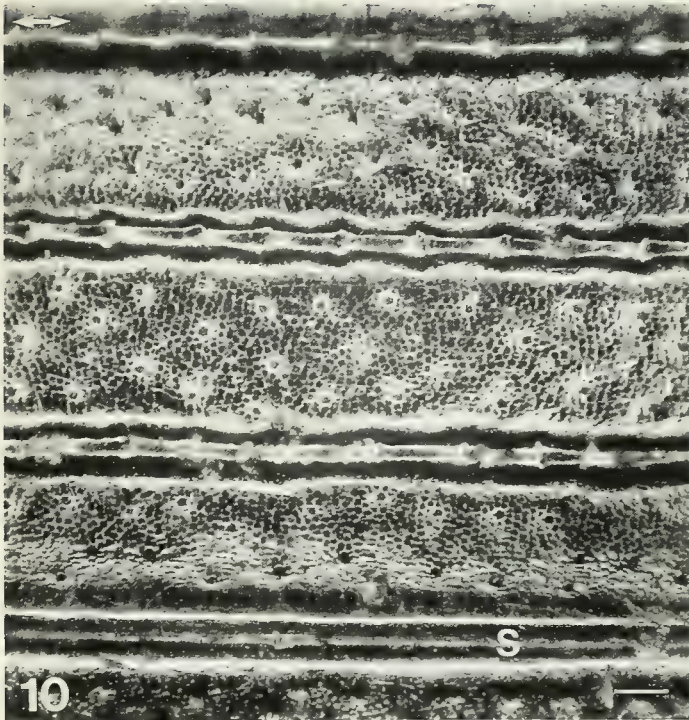
I would like to thank Dr. O. Merkl, Zoological Department of the Hungarian Natural History Museum, Budapest, for the loan of the holotype of *Aphodius venyigei* Endr. and for informations about the type locality. Dr. H. Fery, Berlin, sent me one female of the *venyigei*-habitus for study and gave exact collection data. Dr. C. Besuchet, Muséum d'Histoire Naturelle Genève, loaned specimens from the Petrovitz collection. Dr. Z. Stebnicka, Kraków, sent me a few aberrant specimens of *Aphodius varians* and read the manuscript. Dr. W. Schawaller, Staatliches Museum für Naturkunde Stuttgart, was always very indulgent to an inexorable petitioner. Prof. Dr. Habermalz and Mr. Neugebauer, Institut für Wissenschaftliche Mikroskopie der Universität Tübingen, allowed and helped me to work with their Leitz Ortholux 3 incident-light microscope. All photographic laboratory work was carried out excellently by Mrs. M. Hohloch, Zoologisches Institut der Universität Tübingen. The whole manuscript was constructively criticized by Dr. habil. M. Schmitt, Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn.

#### ZUSAMMENFASSUNG

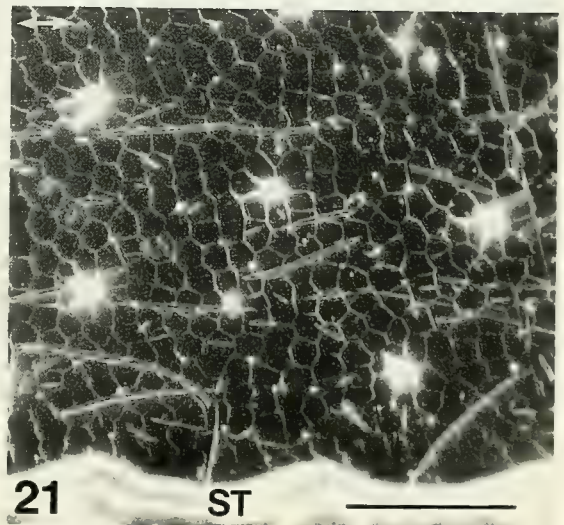
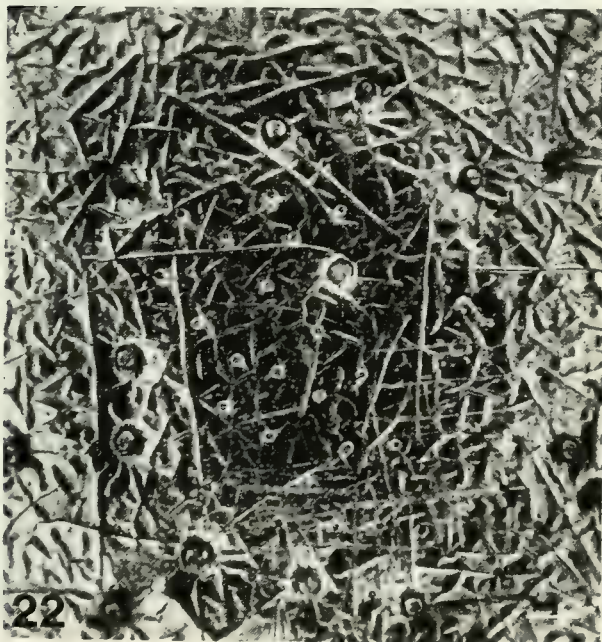
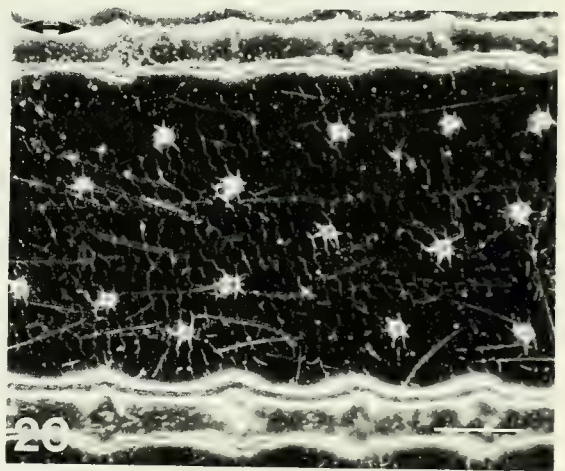
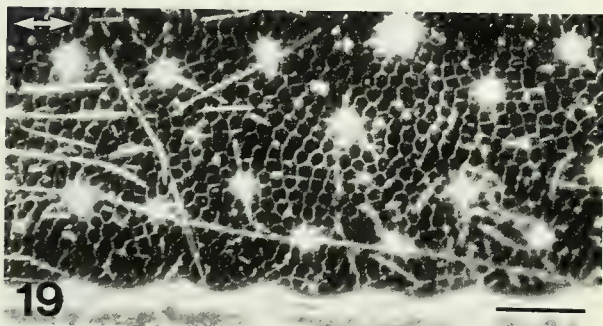
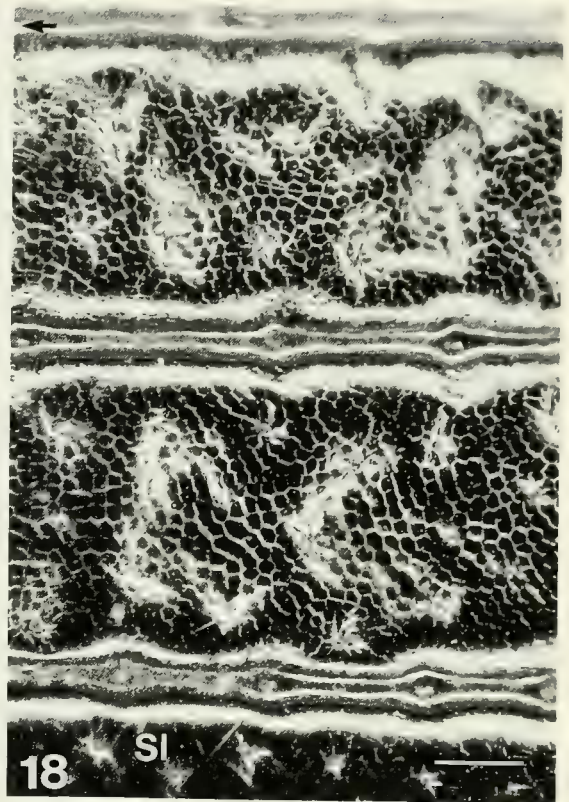
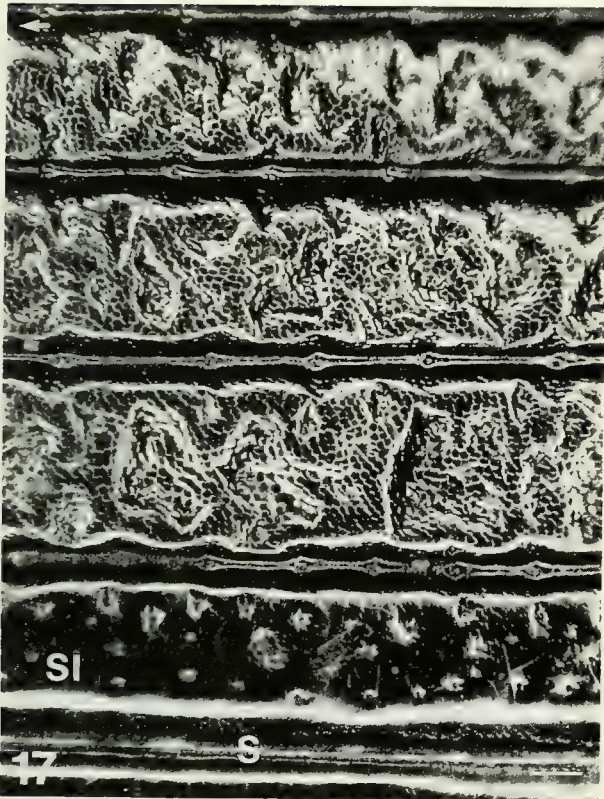
Bei den meisten Insecta und "Myriapoda", bei einigen Crustacea und sogar bei den Loricifera finden wir eine retikuläre Mikroskulptur der Cuticula-Oberfläche. Aufgrund morphogenetischer Überlegungen betrachte ich dieses Muster als ursprünglich für alle Arthropoden- bzw. chitinigen Cuticulae. Das retikuläre Muster gründet auf der ökonomischen, dichtesten Packung der Epidermiszellen. Die Retikulation kann in ein alveoläres Muster modifiziert werden durch Aufwölbung der Polygonoberflächen, hervorgerufen durch eine nicht gespannte Epidermis während der Sezernierung der Epicuticula. Bei den Elytren verschiedener Individuen von *Aphodius (Nialus) varians* Duftschmid (Insecta: Coleoptera: Scarabaeidae: Aphodiinae) finden wir retikuläre und alveoläre Muster neben vielen Übergansformen. Die Mikroskulptur der Oberfläche der Cuticula ist demnach intraspezifisch nicht konstant. Unter Berücksichtigung morphologischer und ökologischer Befunde wird die Form mit extrem alveolären Muster, *Aphodius (Nialus) venyigei* Endrődi, zur Morphe von *A. varians* degradiert. *Aphodius (Melinopterus) reyi* Reitter wird erstmals in Griechenland nachgewiesen.

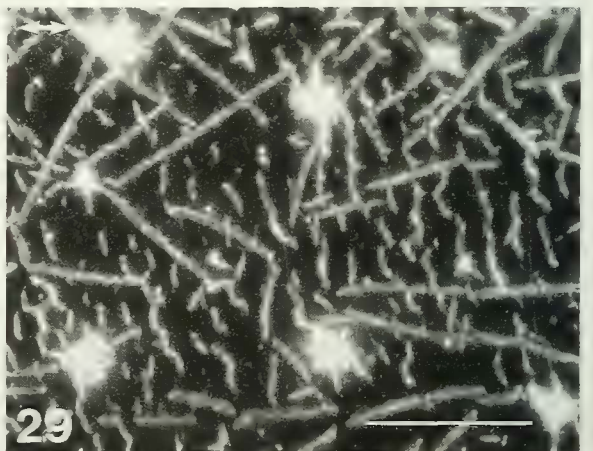
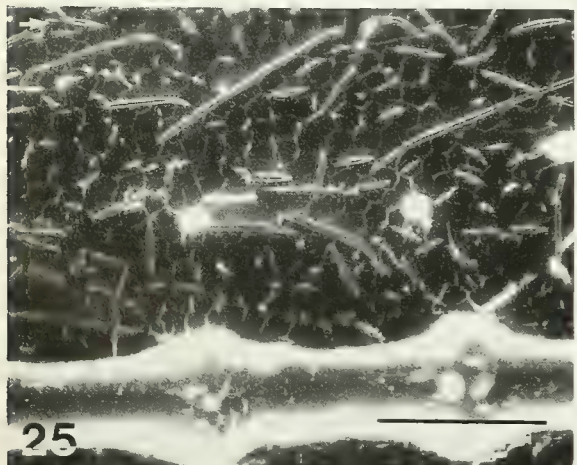
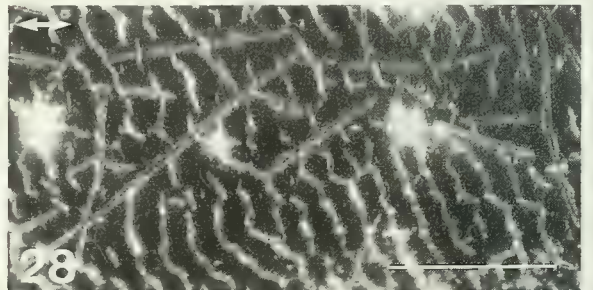
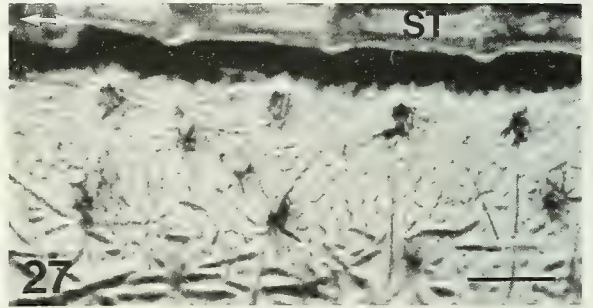
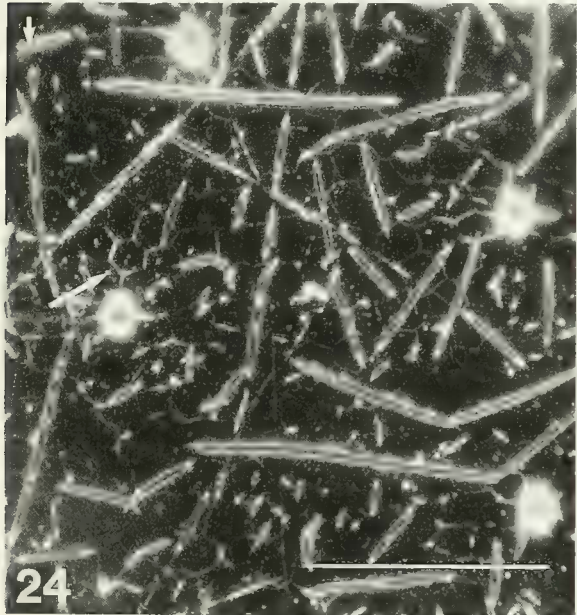
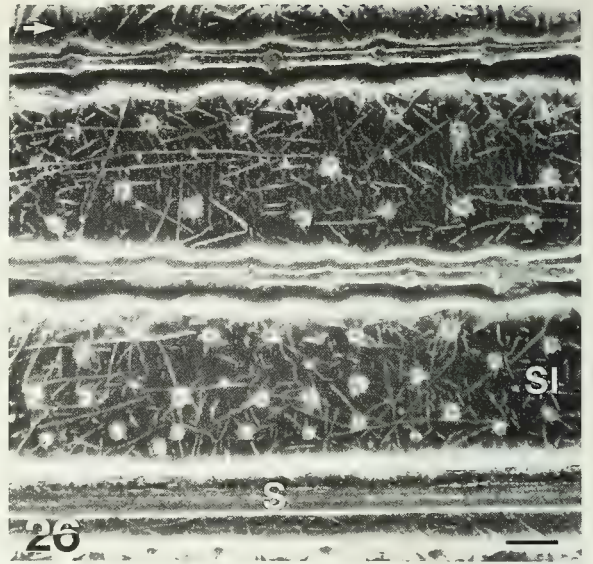
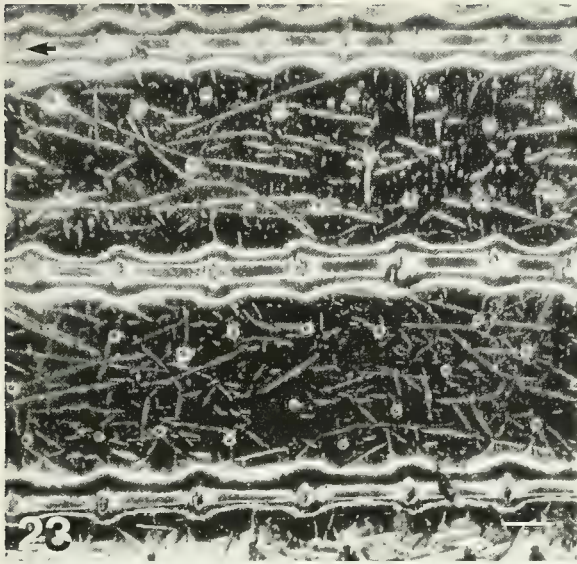


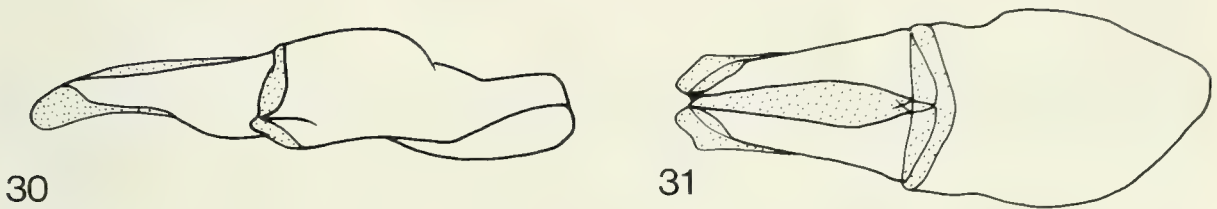












## FIGURES:

FIGS 1-4: *Aphodius varians* morph *venyigei* Endrődi, Holotype, ♂, No. 1. - 1: right elytron and sutural interval of the left elytron; S: elytral suture; IR: irregularity. - 2: right elytron, second interval near the scutellum. - 3: pronotum, discal, double punctate. - 4: caudodorsal part of the caput; T: epicranial tubercle; P: pronotum; M: transparent, craniomarginal zone of the pronotum. - By accident, some topographical data of the photographs were lost. Therefore, the topographical precision is not consistent in all photographs. However, this does not impair their meaningfulness and significance for the present study because the integumental antero-posterior polarity (CALS 1973) is not studied and is not significant in the present case. The orientation of the photographs conforms to the perspective, not to correspondence. The cranial-caudal direction is indicated by double arrows placed in the left upper corner of each photograph. If the cranial direction can be determined, the arrow points craniad only. The scale, placed in the right lower edge, is always 50 µm.

FIGS 5-9: *Aphodius varians* morph *venyigei* Endrődi, ♀, No. 2. - 5: right elytron, cranial third, second to fifth interval. - 6: elytron, non-sutural interval. - 7: pronotum, discal. - 8-9: left elytron, second interval; ST: stria. - Scale = 50 µm.

FIGS 10-16: *Aphodius varians* morph *rugosopunctatus* Petrovitz, holotype, No. 3. - 10: left elytron; S: elytral suture. - 11: left elytron with mechanically induced scratches (by forceps), second and third interval, just behind scutellum. - 12: left elytron, anterior half, second or third interval. - 13: left elytron. - 14: left elytron, second interval, just behind scutellum, anterior to fig. 11. - 15-16: left elytron, median part. - Scale = 50 µm.

FIGS 17-18: *Aphodius varians* Duftschmid, ♀, No. 4. - 17: right elytron, first (sutural) to fourth interval; S: elytral suture; SI: sutural interval. - 18: right elytron, first to third interval; SI: sutural interval. - 19-21: *Aphodius varians* Duftschmid, ♀, No. 5. - 19: second elytral interval. - 20: right elytron. - 21: right elytron; ST: stria. - 22: *Aphodius varians* Duftschmid, ♂, No. 6, pronotum, central-discal. - Scale = 50 µm.

FIGS 23-25: *Aphodius varians* Duftschmid, ♂, No. 6. - 23: left elytron, second to fourth interval, just behind scutellum. - 24: left elytron, third interval, in the middle of the elytron (arrow: polygons). - 25: left elytron, third interval, at the end of the cranial third. - 26-29: *Aphodius varians* Duftschmid, ♂, No. 7. - 26: left elytron, first and second interval; S: elytral suture; SI: sutural interval. - 27: left elytron, high reflecting illumination; ST: stria. - 28: right elytron. - 29: elytron. - Scale = 50 µm.

FIG. 30-31: Aedeagus of *Aphodius varians* morph *venyigei* Endrődi, holotype. - 30: lateral view. - 31: dorsal view.

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